PORIFERAN AFFINITIES OF MESOZOIC STROMATOPOROIDS

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ABSTRACT. The finding of calcite and pyrite spicule pseudomorphs of monaxon spicules in six genera of Mesozoic stromatoporoids confirms poriferan affinities for at least some representatives of this group. Previously, the systematic position has been speculated upon solely from the internal organization of the skeleton.

STROMATOPOROIDS, tabulates, and chaetetids have achieved some notoriety owing to their proposed reclassification from the Cnidaria to the Porifera on the basis of their morphological similarity to some recently discovered sponges, the sclerosponges, which possess both a calcareous and a spicular siliceous skeleton (Hartman 1969, 1979; Hartman and Goreau 1970, 1972). Evidence in the form of spicule pseudomorphs has confirmed the poriferan affinity of chaetetids (Gray 1980; Kazmierczak 1979), and possibly some tabulates (Kazmierczak 1984), but the biological standing of stromatoporoids has remained problematic (for example, see Kazmierczak and Krumbein 1983; Mori 1984; Stearn 1972).

MATERIAL EXAMINED

Several specimens of Mesozoic stromatoporoids that contain spicule pseudomorphs have been found in the collections of the late R. G. S. Hudson, housed in the British Museum (Natural History). They are from the Upper Jurassic of the Middle East and include several holotypes and paratypes. The same feature has also been found by one of us (J. R.) in an undescribed species of stromatoporoid from the Lower Cretaceous of Spain.

Table 1 summarizes spicular data and information on the age and localities of the specimens. Stratigraphical, geographic, and systematic details are given in the cited references. All the spicules are preserved as pyrite or calcite pseudomorphs, either as styles/acanthostyles or possibly as tylostyles, and are arranged intramurally within the axial zone of the skeletal elements. The pyrite pseudomorphs are found as aggregates or chains of crystals arranged along the length of the spicules similar to previously described fossil chaetetid and sclerosponge spicules (Gray 1980; Kazmierczak 1979). These pseudomorphs are found in large numbers, towards the outer edge of the specimen where their original siliceous mineralogy has been replaced, probably as a result of the prolonged leaching by iron-rich pore-waters (Pl. 35, figs. 3 and 4).

The calcite pseudomorphs appear as rods of monocrystalline calcite of a higher transparency than the surrounding microstructural fibres, and are generally preserved in the central areas of the specimen. In *Dehornella crustans* Hudson, where both pyritic and calcitic pseudomorphs are found, the length of the pyrite type is considerably reduced, indicating that pyritization has occurred after partial dissolution of the spicules, producing imperfect replacement, especially of the distal tips. In species where both pseudomorph mineralogies are found, or where obvious corrosion has taken place, only the maximum figures are given. These figures, therefore, certainly represent reduced dimensions of the original spicules.

According to the most recent classification of Mesozoic stromatoporoids (Hudson 1960), all the spiculate species belong to the Milleporellicae, except *Actinostromarianina lecompti* Hudson, which belongs to the Actinostromariicae.

The skeleton of the Milleporellicae consists of fascicular-fibrous microstructure, connected by thin

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tabulae of granular microstructure. There is no lamellar development. The spicules found in these have tapering points, and diverge distally, subparallel to the fibres of the columns (Pl. 35, figs. 1–3). Pseudomorphs do not project into the lumina, and are found singly or in assemblages. Such isolated clusters appear to be remnants of a much denser spicule skeleton, the sporadic distribution of which is now diagenetically determined.

In the Actinostromariicae there is no microstructural differentiation of the pillars and lamellae. The reticulum forms a rectangular meshwork where the elements have a granular central zone and an orthogonal fibrous outer zone. Tabulae of granular microstructure are secreted across the interskeletal spaces. In *A. lecompti* the pseudomorphs are long and thin. They are probably tylostyles, with possible bosses at their proximal end (Pl. 35, fig. 5). The calcite and pyrite pseudomorphs occur side by side and are found both within the pillars and lamellae, where they are generally aligned subparallel to the growth axis of the skeleton. The spicules are evenly distributed, irrespective of their position relative to the skeletal elements. Pseudomorphs can be seen to project into the interskeletal spaces or to terminate abruptly at the skeletal surface due to the corrosion of the projecting length. The spicular positioning appears to form the framework for the subsequent secretion of the calcareous skeleton (Pl. 35, fig. 6).

CONCLUSIONS

The size and distribution of the spicules and the microstructure and arrangement of the calcareous skeleton of these species of Mesozoic stromatoporoid show similarities to representatives of the sclerosponge genera *Murania* (Kazmierczak 1974), *Astrosclera*, *Ceratoporella* (Hartman 1969; Hartman and Goreau 1970, 1972), and *Calcifibrospongia* (Hartman 1979). The systematic position of the sclerosponges is open to question. Some workers (Vacelet 1970, 1985; Levi 1973) believe that the sclerosponges form a polyphyletic and unnatural group and that the members can be better placed in the pre-existing taxa of the Demospongiae. It is likely that the sphinctozoans, tabulates, and the stromatoporoids are also unnatural groupings and that the finding of spicules will enable the construction of a more meaningful classification and phylogenetic reconstruction of these convergent groups. However, spicules cannot be used as a species-specific characteristic due to the rarity of their preservation.

The positive placing of at least some representatives of the stromatoporoids in the Porifera has several other consequences. The terminology, at present based on cnidarian nomenclature, will have to be revised and a classification that, where possible, incorporates spicule data needs to be developed. This will enable stromatoporoids to be studied from a biological standpoint, and allow a valid appraisal of their ecological role as locally significant faunal elements in Mesozoic carbonate buildups.

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EXPLANATION OF PLATE 35

Figs. 1–6. Spiculated Mesozoic stromatoporoids; transmitted light photomicrographs of thin sections. 1, *Dehornella crustans* (Hudson), H5170c. Calcite pseudomorphs of style/acanthostyle spicule arranged subparallel to the microstructural fibres of the calcitic skeleton. × 100. 2, *Dehornella n. sp.*, H5478a. Calcite pseudomorphs of style/acanthostyle spicules arranged in ?lattice. × 175. 3, *Parastromatopora libani* (Hudson), H4789. Large numbers of pyrite pseudomorphs in outer leached zone. × 10. 4, detail of individual pseudomorphs of specimen shown in fig. 3. × 600. 5, *Actinostromarianina lecompti* (Hudson), H4608a. Pyrite pseudomorphs of ?tylostyle spicules. × 330. 6, Spicule framework of specimen shown in fig. 5. × 50.


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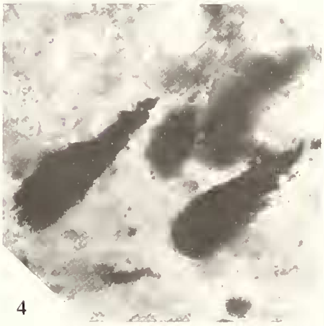
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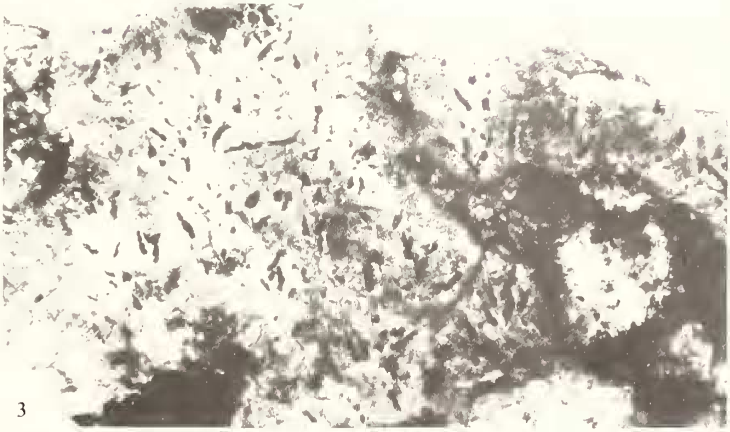
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TABLE 1. *Specimen and spicule data*

Species	Age	Locality	Calcareous skeleton			Spicular data					References
			Gross morphology	Micro-structure	Traces of aquiferous system	Type	Distribution	Present mineralogy	Dimensions		
									Length (μm)	Diameter (μm)	
H *Dehornella crustans* H5170c H5168a	L. Kimm.	Makhtesh Haithira, Israel	Nodular, encrusting	Fasc. Fib.	Astrorhizae	Style	Intramural s.m.	Calcite and pyrite	90–135	13·5–17·0	Hudson (1960)
H *Dehornella n. sp.* H5478a and b	U. Apt.	Ereño, Spain	Laminar, encrusting	Fasc. Fib.	Astrorhizae	Style acanthostyle	Intramural s.m.	Calcite	75–250	5–20	Reitner, pers. obs.
H *Steineria somaliensis* H4897b	L. Kimm.	Makhtesh Haithira, Israel	Dendroid	Fasc. Fib.	Tabulate oscula ?astrorhizae	Style	Intramural s.m.	Pyrite	15–25	6·5–9·0	Hudson (1955*a*)
Shuqraia hethira H5034a	L. Kimm.	Wadi Haithira, Israel	Dendroid	Fasc. Fib.	Astrorhizae	Style	Intramural s.m.	Pyrite	60–80	5–7	Hudson (1955*a*)
Parastromatopora libani H4789	M. Kimm.	Toumatt, Lebanon	Massive, nodular	Fasc. Fib.	Astrorhizae	Style	Intramural s.m.	Pyrite	60	18	Hudson (1954)
H *Promillepora kurnubi* H4898	L. Kimm.	Makhtesh Haithira, Israel	Dendroid	Fasc. Fib.	Tabulate oscula ?astrorhizae	Style	Intramural s.m.	Pyrite	50	12	Hudson (1955*a*)
P *Actinostromarianina lecompti* H4608a and b	U. Kimm.	Alam Abyadh, Arabia	Nodular, encrusting, fasciculate	Granular and orthogonal	Astrorhizae	?Tylostyle	Intramural s.s.	Calcite and pyrite	180	8	Hudson (1955*b*)

H = holotype; P = paratype; Fasc. Fib. = Fascicular Fibrous; s.m. = subparallel to microstructural fibres; s.s. = subparallel to growth axis of skeleton. Specimen numbers refer to the R. G. S. Hudson Collection housed in the British Museum (Natural History).

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